

A comparison of the energy budgets of two freshwater Pulmonates: *Lymnaea peregra* (Müller) and *Physa acuta* (Drap.)

by

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With 5 figures

ABSTRACT

The energy budgets of two freshwater gastropods, *Lymnaea peregra* and *Physa acuta*, were compared in similar experimental conditions (20°C, fed *ad libitum* with 24 h-decayed lettuce), and found to differ in several ways. 1) *L. peregra* has a higher assimilation efficiency than *P. acuta* (72% vs 60%). 2) These species assimilate different components of the ingested food: *P. acuta* uses a smaller, but more energetic part (probably mainly bacteria), whereas *L. peregra* assimilates a larger, but less energetic part (probably mainly cellulose). 3) *L. peregra* allocates more of its assimilated energy to oxygene consumption and mucus production (maintenance investments), whereas *P. acuta* invests more in growth and reproduction (production investments). Such differences are relevant to the natural habitat of these two species: *P. acuta* colonizes warm, eutrophic and temporary pools, where decaying material constitute the main part of available resources, and where adult mortality is high and unpredictable. By contrast, *L. peregra* is frequently found in colder, oligotrophic and predictable environments, where living primary producers constitute the main part of available resources, and where biotic interactions are important factors of mortality.

INTRODUCTION

The two freshwater Pulmonates *Physa acuta* (Drap.) and *Lymnaea peregra* (Müll.) are widespread European species, which however are rarely found together. *L. peregra* is a largely distributed species, usually living in cold, oligotrophic and permanent habitats

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such as lakes and rivers, whereas *P. acuta* is an opportunistic species, colonizing warm, eutrophic and temporary pools (PERRIN 1986).

Under similar laboratory conditions, significant and presumably adaptive differences are found in their life-history strategies: comparing with *L. peregra*, *P. acuta* has a higher growth rate, is more fecund, and lays relatively larger eggs. Consequently, its generation time is shorter, and its per capita rate of increase is higher (CALOW 1981, PERRIN 1986). As such life-history features directly depend on the energy budget, these species presumably differ in their resource acquisition and allocation strategies.

In this paper we compare the energy budgets of the two species under similar experimental conditions to examine the energetic significance of the differences in their life-history strategies.

MATERIAL AND METHODS

L. peregra occurs in a wide range of altitudes. The individuals under study originated from three localities differing in water temperature and length of the growing season: LP1, a lowland pond (286 m, 45°95'N, 5°03'E), LP2 a lowland stream (440 m, 46°43'N, 6°34'E) and LP3 a high altitude lake (1690 m, 46°20'N, 7°04'E). *P. acuta* shows less ecological variability, occurring preferentially in warm, eutrophic temporary pools. The individuals under study originated from a lowland temporary pond (360 m, 46°55'N, 4°78'E).

All the snails were reared at 20°C in reconstituted water (Table 1) and fed *ad libitum* with previously weighted lettuce. Unlike *L. peregra*, *P. acuta* is unable to ingest fresh lettuce. Therefore, lettuce given to both species was previously frozen, and allowed to decay 24 h before given to the snails. Food was daily renewed, rests and faeces were collected, dried for 24 h at 60°C, and weighed. Daily ingestion (I) was obtained as the difference between the energy content of lettuce given one day (D), and that of rests collected the following day (NI):

$$I = D - NI$$

Similarly, daily assimilation (A) was obtained as the difference between the energy content of ingested food (I) and that of faeces (NA):

$$A = I - NA$$

Each week, shell length and diameter were measured (Mesuroscop V-12 Nikon), eggs were collected, dried (24 h, 60°C) and weighed. Animal dry weight was then calculated from shell measurements using previously established relationships, and production (P) was computed as the sum of animal growth (Pg) and reproduction (Pr):

$$P = Pg + Pr$$

Respiration was measured in a flow through system: from a common tank, oxygen saturated water was pumped both to an animal- and a control chamber. A switch allowed to measure (Polarigraphic Orbisphère ppm-oxygen detector, model 2714) alternatively water from animal and control chamber. Oxygen consumption was obtained by difference.

The energetic value of fresh and 24 h-decayed lettuce, faeces, snails and eggs were determined by a Parr calorimetric bomb (model 1108), using 300-400 mgDW samples. Following CALOW (1981) we assumed the energetic equivalent of oxygen consumption to be 21 Joules/ml O₂. All results will be expressed in Joules rather than mgDW or ml O₂.

All budget components (Y) have been modelled as log-log functions of body energetic content (E):

$$Y = a E^b$$

$$\text{or } \ln Y = \ln a + b \ln E$$

the constant a and b being computed from a classical linear regression program (SPSS Program Library).

RESULTS

Animal dry weight: the following relationships were obtained in estimating animal dry weight (excluding shell) from shell measurements:

$$L. peregra: \quad \ln DW = 1.33 \ln V - 4.23 \quad (r^2 = 0.82)$$

$$P. acuta: \quad \ln DW = 1.00 \ln V - 2.04 \quad (r^2 = 0.87)$$

where DW is dry weight [mg], $V = (L/2)^2 \pi D$, L is shell length [mm], and D is shell diameter [mm].

Energetic values: The dry matter and energy content of lettuce is given in Table 2. As can be seen, the energy content increases significantly ($p < 0.001$ for the difference between 0 h and 24 d decay, t -test for small samples) as a result of bacterial activity, and then rapidly levels off. The value obtained after 24 h decay was used to compute the energetic value of ingested lettuce.

The energy content of animals (excluding shell), faeces and eggs are given in Table 3 for both species. All interspecific differences are significant (t -test). Rather surprising is the great difference in the body energetic value of these two species.

Energy budgets: the logarithmic values of daily ingestion (I), assimilation (A), respiration (R) and production (P) are plotted against the logarithmic value of body energy content (E) in Fig. 1 to 4. These values were fitted with linear regressions, the coefficients of which are given in Table 4. The daily production of faeces NA [J/d] appeared to be a constant fraction of ingestion I [J/d]:

$$L. peregra: \quad NA = 0.28 I \quad r^2 = 0.76$$

$$P. acuta: \quad NA = 0.40 I \quad r^2 = 0.85$$

The assimilation efficiencies (A/I) are therefore size-independent. *L. peregra* has a higher one (72%) than *P. acuta* (60%). As can be seen on Fig. 1, 2 and 3, *L. peregra* has higher ingestion, assimilation and respiration rates than *P. acuta* on its whole size range, whereas the production rate, i.e. the sum of growth P_g and reproduction P_r investments, is higher in *P. acuta* (Fig. 4). These results are summarized in Fig. 5 a) and b); as can be seen in both species, the assimilation rate is higher than the sum of production and respiration rates. This difference is larger in *L. peregra*, and can be attributed to excretion and mucus production, neither of which was directly estimated.

DISCUSSION

From our results, *L. peregra* and *P. acuta* differ in their resource acquisition and allocation strategies, two aspects of the energy budget which will be discussed separately.

Resource acquisition: the main interspecific differences in resource acquisition strategies concern the assimilation efficiency as well as the energetic content of faeces. Both species have high assimilation efficiencies (72% in *L. peregra* and 60% in *P. acuta*); this is not unusual for gastropods, and assimilation efficiencies of 95% (!) have been noted

TABLE 1.

Rearing water: salts [mg] added to 60 l ion-free water

Salts	Quantity
KHCO3	1000
NaNO3	1000
K2PO4	1000
MgSO4 (7H2O)	983
CaCl2 (2H2O)	2120

TABLE 2.

Dry matter content (DM) and energetic content (E) [J/mgDW] of fresh and decayed lettuce

	0 h decay	24 h decay	48 h decay
DM	5.4 ± 0.9 (n = 30)	3.7 ± 0.4 (n = 8)	3.7 ± 0.4 (n = 8)
E	16.23 ± 0.41 (n = 3)	19.55 ± 0.18 (n = 3)	19.29 ± 0.76 (n = 3)

TABLE 3.

Energetic content [J/mgDW] of snails, faeces and eggs of animals of both species

	Snails	Faeces	Eggs
<i>L. p.</i>	16.72 ± 1.11 (n = 7)	18.05 ± 0.11 (n = 5)	18.48 ± 0.25 (n = 3)
<i>P. a.</i>	20.75 ± 0.20 (n = 4) p < 0.001	15.52 ± 0.22 (n = 4) p < 0.001	17.58 ± 0.05 (n = 3) p < 0.01

TABLE 4.

Coefficient values of the log-log regressions of ingestion (I), assimilation (A), respiration (R), and production (P) [J/d] as functions of body energetic content [J]

		Intercept	Slope	r ²
<i>P. a.</i>	I	0.63	0.70	0.86
	A	0.12	0.70	0.75
	R	-1.47	0.63	0.92
	P	-4.29	1.29	0.76
<i>L. p.</i>	I	2.51	0.37	0.87
	A	2.18	0.37	0.79
	R	-0.09	0.44	0.92
	P	-3.17	0.83	0.74

in species of this group (CALOW 1975). *L. peregra* however has a higher one, whereas its faeces have a significantly higher energy content (18.05 vs. 15.52 J/mgDW).

From these results it can be inferred that the species under study assimilate different parts of the same food. The ingested lettuce is made of several components, with different energetic values; *L. peregra* assimilates a large, but less energetic component; therefore, assimilation efficiency is relatively high, and faeces are relatively more energetic. *L. peregra* probably mainly feeds on the cellulosic part of ingested lettuce. This species possesses a high cellulasic activity, and is able to digest green algae which thick cell walls (CALOW 1970, 1975).

By contrast, *P. acuta* assimilates a smaller but more energetic part of ingested lettuce; therefore, assimilation efficiency is weaker, and faeces are less energetic. In fact, *P. acuta* most probably feeds on bacteria developing on decaying lettuce, which are more energetic than lettuce itself, as can be seen on Table 2. This would explain why this species does not feed on fresh lettuce. Indeed, species of this genus seem specialized on detritus (e.g. HESLER *et al.* 1986).

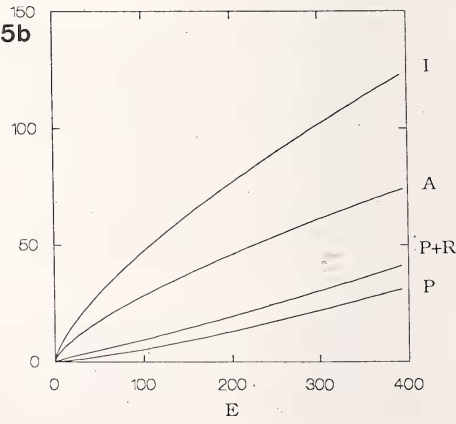
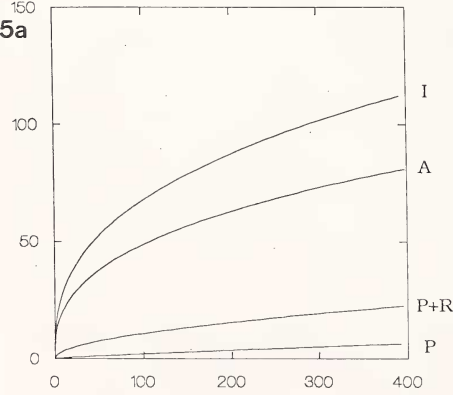
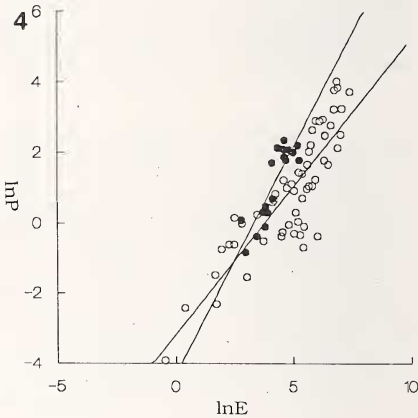
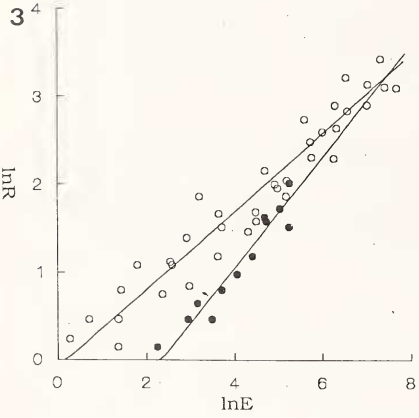
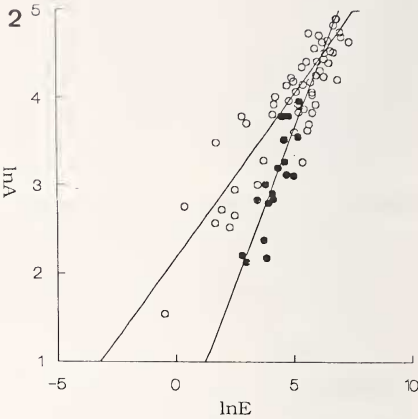
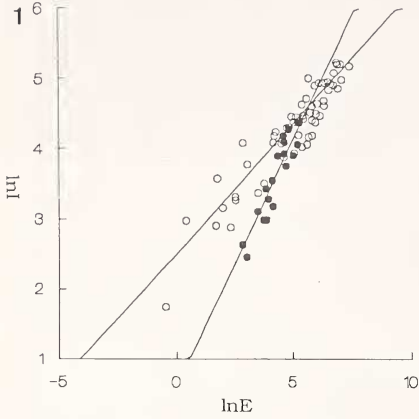
Such differences are relevant to the habitat of both species. *P. acuta* lives in warm, eutrophic pools where decaying material may constitute an important part of available resources. By contrast, *L. peregra* often lives in colder, oligotrophic environments, with less organic production: a higher assimilation efficiency may be adaptive in such environments, as well as the ability to consume directly primary producers, and to digest cellulose.

Resource allocation: It will be meaningful here to distinguish the energy allocated to production, from that allocated to organism's maintenance. Allocation to production is easy to estimate from the sum of growth and reproductive investments. Allocation to maintenance will be estimated from metabolism, excretion and mucus production. The reason to consider mucus production as a maintenance investment, is that mucus plays a role in organism's locomotion, resource acquisition and predator avoidance, in calcium adsorption (SCHLICHTER 1981), elimination of toxic components such as ammonium and protection against physico-chemical variations (SULLIVAN & CHENG 1975 *in* BUBEL 1984). In mucus are also found pheromones which inhibit growth and reproduction in conspecifics (CAMERON & CARTER 1979, ROLLO & WELLINGTON 1981, CHAUDHRY 1986 *on Physa sp.*).

The production of mucus was not directly estimated in present work. However, the difference between the observed assimilation and the sum of growth, reproduction and respiration rates is to be attributed to excretion and mucus production. This difference represent 47% of ingested energy (60% of assimilation) in adults *L. peregra* and 34% (57% of assimilation) in adults *P. acuta*. These values in fact essentially represent mucus production, for excretion does not usually exceed 1% of ingested energy. Such values of mucus production are not unusual in gastropods (CALOW 1974) and others mucus producers. For example, the mucus production reaches 70% of ingestion in a freshwater flatworm (TEAL 1957 *in* CALOW 1977) and 66 to 74% of assimilation in a Polyplacophoran (HORN 1986).

From present results, *L. peregra* invests more than *P. acuta* in mucus production. This is equally true for metabolism (table 4 and Fig. 3). Both regressions fit very well the data and these results are consistent with previous measurements by BERG and OCKELMAN (1959) on *L. peregra*, who obtained at 18°C:

$$\ln R = 0.08 + 0.59 \ln WW,$$



where WW is the wet weight of snails excluding shell, and R is expressed in $\mu\text{l/h}$. Converted in the same units, our results are:

$$\ln R = -0.01 + 0.595 \ln WW$$

L. peregra seems therefore to invest a higher proportion of assimilated energy in organism's maintenance (mucus production and metabolism). By contrast, our results indicate that, from a given amount of assimilated energy, *P. acuta* invests more in production (Table 4 and Fig. 4). This allows this species to attain a higher growth rate, and to reach maturity sooner. These differences again are relevant to the habitat of both species: *L. peregra* lives in predictable environments presenting annual variations, and dominated by biotic interactions. The adaptive response of this species is to be univoltine and to put a premium on organism's maintenance, predator avoidance and competitive ability. By contrast, *P. acuta* lives in more productive environments, with few predators and competitors, but unpredictable and density-independent adult mortality (eggs and juveniles are able to survive in mud soil). The adaptive response of this species is to put a premium on growth and reproduction, and to be bivoltine when possible.

FIGURE 1.

Log-log regressions of daily ingestion ($\ln I$) vs. body energetic content ($\ln E$) in *L. peregra* (open circles) and *P. acuta* (black circles).

FIGURE 2.

Log-log regressions of daily assimilation ($\ln A$) vs. body energetic content ($\ln E$) in *L. peregra* (open circles) and *P. acuta* (black circles).

FIGURE 3.

Log-log regressions of daily respiration ($\ln R$) vs. body energetic content ($\ln E$) in *L. peregra* (open circles) and *P. acuta* (black circles).

FIGURE 4.

Log-log regressions of daily production ($\ln P$) vs. body energetic content ($\ln E$) in *L. peregra* (open circles) and *P. acuta* (black circles).

FIGURE 5.

Daily energy budgets of *L. peregra* (a) and *P. acuta* (b) vs. body energetic content (E). I = ingestion, A = assimilation, P + R = production plus respiration, P = production.

RÉSUMÉ

Les budgets énergétiques de deux Pulmonés dulcicoles, *Lymnaea peregra* et *Physa acuta* ont été comparés en conditions expérimentales (20°C, nourrissage *ad libitum* de salade préalablement congelée et légèrement décomposée). Les différences suivantes ont été notées: 1) *L. peregra* possède une meilleure efficacité d'assimilation que *P. acuta* (72% contre 60%). 2) Les composants assimilés diffèrent: *P. acuta* assimile une part plus faible, mais plus énergétique (probablement composée principalement de bactéries), alors que *L. peregra* assimile une part plus importante mais moins énergétique (probablement constituée en grande partie de cellulose). 3) *L. peregra* alloue une plus grande part de l'énergie assimilée à la consommation d'oxygène et à la production de mucus (investissements de maintenance) alors que *P. acuta* investit davantage en croissance et en reproduction (investissements de production).

Ces différences sont mises en relation avec l'habitat naturel des deux espèces: *P. acuta* est une espèce colonisatrice, qui habite volontiers les mares eutrophiques et temporaires, où la matière organique en décomposition fournit le gros de la nourriture disponible, mais où la mortalité adulte est forte et imprévisible. *L. peregra* par contre s'observe en milieux plus froids, oligotrophes et stables, où la consommation directe de producteurs primaires peut être avantageuse, et où les interactions biotiques constituent une importante cause de mortalité.

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